An Adaptive Dynamic Model of a Vigilance Game in Group Foragers

Undergraduate Research Thesis

Presented in partial fulfillment of the requirements for graduation *with honors research distinction in zoology* from the College of Arts and Sciences at The Ohio State University

by

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Abstract

There is a well observed relationship between group size and time spent being vigilant in group foragers. The many eyes hypothesis supposes that individuals exhibit lower vigilance in larger groups because of the benefit they get from the vigilance of others. In the past, models which try to provide a mechanism in support of the many eyes hypothesis do not capture the way group size depends on vigilance, and some models depend on the idea that individuals perceive the strategies of all other group members, called "behavioral monitoring." Here I present a game theoretical model for vigilance using adaptive dynamics and pairwise invasion which captures this relationship, includes the way group size changes with vigilance and, removes the need for behavioral monitoring. By approximating a fitness function for an individual using a particular vigilance strategy in a group of size N, I can show when new strategies of vigilance will invade using pairwise invasion analysis. Using this analysis, I construct a dynamical system which describes the change in group size and vigilance as they relate to each other. By spanning the entire parameter space I show that at equilibrium, larger groups have far more limited maximum vigilance. Furthermore, by varying intraspecific competition I show an inverse relationship between group size and vigilance. Thus I provide a mechanism in support of the many eyes hypothesis from an evolutionary game theory perspective.

Introduction and Biological Background

Vigilance is the act of visually scanning the environment for predators. While vigilance and foraging may occur contemporaneously in some species, (Blanchard and Fritz 2007), typical group foragers, when scanning for food, do not scan the landscape for predators. It is well understood, therefore, that vigilance is costly (Bernard 1980) for a wide range of foragers from birds (Lendrem 1983, Fritz et al. 2002) to ungulates (Illius and Fitzgibbon 1994). An individual choose to either be focused on foraging or focused on being vigilant. For the most part, as in the studies listed above, active vigilance reduces foraging rate significantly. For an individual, simple optimization tell us that, if there is a tradeoff between foraging and vigilance, the optimal allocation to vigilance is wherever the marginal benefit of vigilance is equal to the marginal cost of not foraging.

In a group, this optimal allocation of vigilance becomes more complicated, because other individuals in the group may be vigilant and alert neighboring individuals, to some degree, by fleeing (Davis 1975, Proctor et al. 2001).How, then, should group foragers allocate their time in foraging and vigilance and how does group size interact with that decision? The pure vigilance strategy, wherein all group members are vigilant all the time, is almost always vulnerable to invasion by any mutant strategy with a non zero amount of foraging because that mutant individual increases fitness by foraging without incurring very much risk, as they can still rely on other group members to spot a predator. The pure foraging strategy, wherein all individuals spend all of their time foraging is also often vulnerable to invasion. The life-dinner principal (Dawkins and Krebs 1979), which says that the selective pressures on strategies preserving life are stronger than those of finishing a meal, predicts that the cost from lost foraging time will be less than the benefit from vigilance.

For group foragers this behavior is well studied, and it is well understood that there is a relationship between group size and vigilance. As group size increases vigilance decreases (Sansom et al. 2008, Blank 2018, van der Marel et al. 2019). The prevailing, not mutually exclusive hypotheses are the "many eyes hypothesis," in which more individuals being vigilant decreases risk of attack to each individual and each individual reacts to the decreased risk by decreasing their vigilance time (Elgar 1989), and "encounter

dilution" which describes how the risk of any one individual being attacked decreases in larger groups by virtue of there being more individuals a predator could attack. Our intuition about the many eyes hypothesis leads us to the right conclusion but may be misleading because we assume that all group members have a shared understanding of strategy and a common reaction to a single detection event. This shared understanding is called "behavioral monitoring"(Lima 1995a), where an individual perceives the strategies being employed by all other individuals and uses that information to make decisions. The common reaction, called "collective detection" (Lima 1995b) is when a whole group will necessarily flee when a single individual detects a predator. There are existing models which support the many eyes hypothesis (Pulliam et al. 1982, Lima 1987, McNamara and Huston 1991,), but they often depend on these ideas of behavioral monitoring and collective detection which do not have strong empirical support (Lima 1995a, Roberts 1998). Here I avoid arguments of behavioral monitoring for vigilance but instead look at this game through the lens of behavior evolution, initially thinking of this process over long time scales with individuals which are not making decisions about vigilance at behavioral timescales but using a constant vigilance strategy. I also consider how similar dynamics may emerge from social learning, on shorter timescales, again without requiring behavioral monitoring.

By constructing an approximation for individual fitness, as a function of vigilance and of group size, I use adaptive dynamics in a pairwise invasion approach (Diekmann 2004, Brännström et al. 2013) to approximate rates of change for both equilibrium vigilance and group size and show a mechanism for the emergence of the relationship between group size and vigilance without relying on behavioral monitoring and loosening the requirement for collective detection.

Model Background

To approximate fitness we consider fitness as it changes through time. That is to say that if w_t is fitness at some time t then

$$w_t = \alpha_t + (1 - \mu_t)w_{t+1} \tag{1}$$

where α_t is the increase of fitness in the time step t and μ_t is the risk of death in that time step (Werner and Gilliam 1984). Noticing that fitness must be maximize $w_{t+1} = w_t$ so by setting these equal to one another we find that individual fitness is

$$w = \frac{\alpha}{\mu} \tag{2}$$

Both α and μ depend on group size and vigilance. For this model V will be proportion of time spent foraging and E will mean proportion of the time spend being vigilant. $E = 1 - V$ clearly, and I will express the model in terms of V. Here I assume that time spent engaging in behaviors other than foraging or vigilance is negligible, insights from this model may not extend to the cases where individuals spend appreciable time performing other social behaviors while foraging, like grooming or mating. Group size will be denoted as N throughout.

First I consider $\alpha(V, N)$. using they Holling II (Holling 1959) functional response I formulate $\alpha(V, 1)$ as

$$\alpha(V, 1) = \frac{s_1 V}{s_2 + V} \tag{3}$$

where s_1 is the foraging rate and s_2 is a constant proportional to handling time. When there are more individuals in a group competition increases and thus foraging rate decreases. To that end, I formulate $\alpha(V, N)$ as

$$\alpha(V, N) = \frac{s_0}{(1 + aV)^{N-1}} \frac{V}{s_2 + V} \tag{4}$$

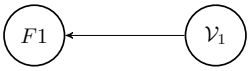
where s_0 is the base foraging rate for an individual and a is the intensity of competition. Another way to consider competition would be to increase S_2 with increased N to capture fights over food, but to keep the computation more manageable, I choose to formulate it as above. For each individual in the group beyond the individual in question, foraging rate is decreased by some factor which depends on the intensity of competition.

To formulate μ, we start by trying understand how antipredator information is spread through a population. We suppose that an individual might respond to another individual's flee response but may not. In this way we loosen the requirement for collective detection. Here I take an elementary probabilistic approach rather than using network diffusion so as to avoid including position in the model. Although a network based approach could be used to produce a highly accurate model of the spread of antipredator information through a group of foragers, as it has been used in fish (Vabø and Nøttestad 1997), this would complicate the model beyond what is necessary for our discussion of vigilance and group size. Using the probabilistic approach makes the assumption, then, that the foraging group is well mixed and no individual is spending a disproportionate amount of time on the periphery.

Using the probabilistic approach, the spread of antipredator information μ can be considered the probability of an individual not fleeing in the event of a predator attacking. For this model we make the assumption that no individual can struggle away from a predator; they can either escape or get killed. I also simplify the model by assuming that all individuals in the group have the same ability to see the predator. First we will consider just the likelihood that an individual does not escape given that there is a predator attacking it.

To illustrate this let us look at examples of groups with one, two, or three individuals. I will illustrate the flow of information in decision trees using "F" to mean fleeing and "$\neg F$" to mean not fleeing. I also use "$\mathcal{V}$" to mean seeing, and "C" to mean communicating. Additionally I write P_v to mean probability of seeing a predator while being vigilant at any particular moment, and P_N to mean the likelihood of perceiving and acting on another individual's flee response.

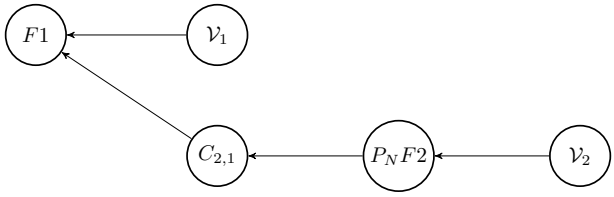
In the trivial example of a one member group the only way for the individual to flee is if it sees the predator so the flow of information looks like



and, because we know that the likelihood of seeing a predator is the product of P_v and the proportion of the time spent looking $(1 - V)$ we write the likelihood of not fleeing as

$$\neg F1(V) = 1 - P_v(1 - V) \tag{5}$$

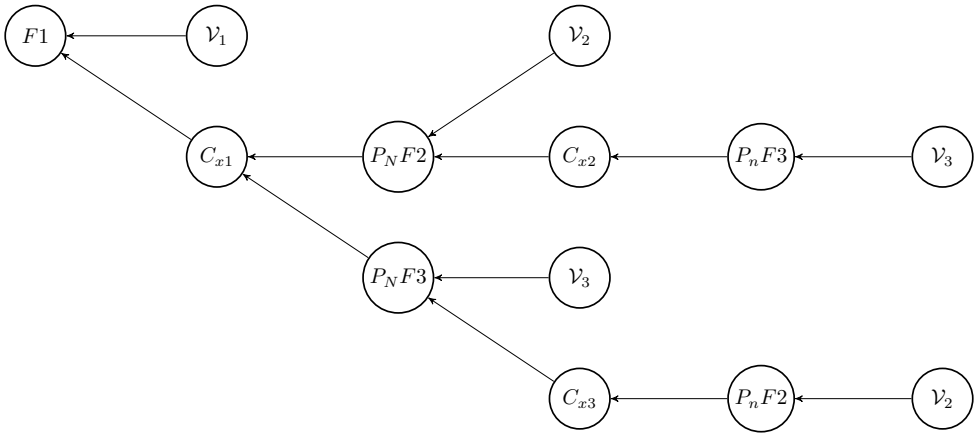
Now consider an example with a group of size 2 with individuals "1" and "2." Again we investigate the likelihood of "1" not fleeing by first looking at the schematic for information flow. In this case, "1" may either see the predator or see "2" flee and follow suit. In the latter case, "2" must be fleeing because it saw the predator itself, because we know "1" did not. The schematic looks like this



From this we see that to write the likelihood of "1" not fleeing we consider the product of "1" not seeing the predator and "1" not being alerted by its neighbors that there is a predator. We see that "1" being alerted to the presence of a predator is the product of "2" fleeing and "1" trusting that information. Thus we can write $\neg C_{2,1} = 1 - P_N F2(V)$ which by DeMorgan's Law or some rearrangement is $(1 - P_N) + (P_N \neg F2(V))$. We also notice that because 2 can only flee because it sees the predator we have reduced the schematic to the case of size 1. That all means we can write that as

$$\begin{aligned} \neg F1(V) &= (1 - P_v(1 - V))(\neg C_{2,1}) \\ &= (1 - P_v V)((1 - P_N) + P_N \neg F2(V)) \\ &= (1 - P_v V)((1 - P_N) + P_N(1 - P_v(1 - V))) \end{aligned} \tag{6}$$

As a final example we look at a group of size 3 and we are interested in an arbitrary individual we will call "1" and it's likelihood of fleeing. Individual "1" may flee because it sees a predator ($\mathcal{V}_1$) or because it sees a group member fleeing ($C_{x,1}$). If the latter is true "1" saw "2" or "3" fleeing. The likelihood of "1" observing "2" fleeing is the product of the likelihood of "2" fleeing (F_2) and the likelihood that "1" trusts that information (P_N). Likewise, likelihood of "2" fleeing is found in a similar manner. Either "2" sees a predator ($\mathcal{V}_2$) or they see another individual fleeing. We know that "1" has not fled so if "2" sees a group member fleeing they must see "3". The only way that "3" can flee, given that "1" and "2" have not seen the predator, is for it to observe the predator itself ($\mathcal{V}_3$). Below is a schematic of the potential paths the information may have taken to get to "1." The only way information can originate is through observation ($\mathcal{V}_x$)



If Individual "1" does not flee it both does not see a predator and it does not react to anyone else fleeing, so we can write

$$\neg F1(V) = (1 - P_v(1 - V))(\neg C_{x1}) \tag{7}$$

$\neg C_{x1}$ is the likelihood that "1" does not see any individuals fleeing or in other words "1" does not see "2" fleeing and it does not see "3" fleeing, which we write $\neg C_{x1} = \neg C_{2,1} \neg C_{3,1}$ which means that our full expression can be written

$$\neg F1(V) = (1 - P_v(1 - V))((\neg C_{2,1})(\neg C_{3,1})) \tag{8}$$

As above $C_{2,1}$ is the product of "2" fleeing and "1" trusting the information so $\neg C_{2,1} = 1 - P_N F2(V)$ which I write as $(1 - P_N) + (P_N \neg F2(V))$. This is the same for $C_{3,1}$.

Thus we rewrite our original expression as

$$\neg F1(V) = (1 - P_v(1 - V))((1 - P_N) + (P_N \neg F2(V)))((1 - P_N) + (P_N \neg F3(V))) \tag{9}$$

It is now helpful to point out that $F2(V)$ and $F3(V)$ are schematically identical, when all individuals have the same likelihood of seeing a predator. In fact $F2(V)$ and $F3(V)$ are simply the schematic reduced to a group size of 2. This means that if we let $\neg F_n(V)$ to mean the likelihood of a particular individual not fleeing in a group of size n, we reduce our expression to

$$\neg F_3(V) = (1 - P_v(1 - V))((1 - P_N) + (P_N \neg F_2(V)))^2 \tag{10}$$

We continue this pattern to see that in general the likelihood for an individual not fleeing in the case of an attack in a group of size N is equal to

$$\begin{aligned} \neg F_N(V) &= (1 - P_v(1 - V))((1 - P_N) + P_N \neg F_{N-1}(V))^{N-1} \\ \neg F_1(V) &= (1 - P_v(1 - V)) \end{aligned} \tag{11}$$

The likelihood of not fleeing in the presence of a predator is the same as risk of death given the presence of a predator. That means we can think of μ as

$$\mu = F_N(V) P_A(N) \tag{12}$$

Where $P_A(N)$ is the likelihood that a predator attacks a particular individual given a group size N. The recursion in this antipredator information scheme makes it difficult to use pairwise invasion analysis, so we seek to find a reasonable and simple replacement which captures the same behavior. We consider several ways to accomplish this.

The most basic approach would be to formulate μ as

$$\mu = (1 - (1 - V)P_v)(1 - (1 - V)P_N P_v)^{N-1} P_A(N) \tag{13}$$

Where P_N is a constant related to the likelihood of transmission (which we can think about as reliability). The next formulations have P_N change as a function of group size. If reliability grows with P_N we formulate that as

$$\mu = (1 - (1 - V)P_v)\left(1 - (1 - V)\frac{N}{C + N}P_V\right)^{N-1} P_A(N) \tag{14}$$

Where C is a positive constant which is inversely related to reliability between two individuals. A reasonable way to think about C is to set $\frac{2}{C+2} = P_N$ and solving for C to get $C = 2\frac{(1-P_N)}{P_N}$. In the case where reliability decreases with group size we formulate μ as

$$\mu = (1 - (1 - V)P_v)\left(1 - (1 - V)\frac{C}{N}P_V\right)^{N-1} P_A(N) \tag{15}$$

Where C is a positive constant directly related to reliability between two individuals. Again we may think of C as the solution to $\frac{C}{2} = P_N$ so clearly $C = 2P_N$. By comparing these three formulations to the output of the recursive function we get an idea of which formulation is most reasonable.

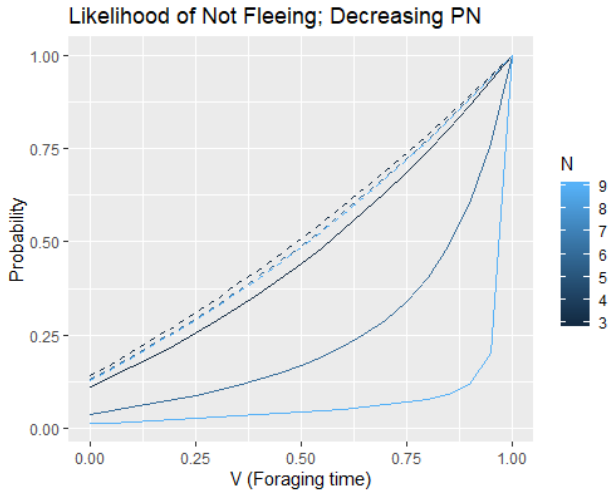


Figure 1 Shows the approximation where P_N decreases with increased group size (Eq. 15). Dashed lines show the approximation, solid lines show the recursive formulation

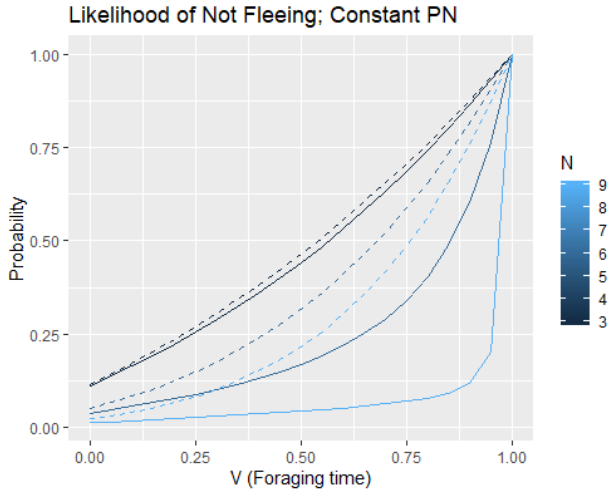


Figure 2 Shows the approximation where P_N is constant (Eq. 13) Dashed lines are the approximation, solid lines are the recursive solution

In the following figures, the recursive solution is shown as a solid line and its analytical approximation is shown as a dashed line. Each figures was produced with $P_v = 0.8$ and $P_n = 0.3$ with the constants, C, calculated as discussed above. The main feature of the recursive solution (Shown as the solid line in Figs. 1,2, and 3) is that as N increases the beginning of the curve becomes flatter and the end of the curve becomes steeper. This illustrates the marginal cost of foraging time in a group. In a large group the marginal cost of foraging is initially very low but becomes very high close to $V = 1$.

If we consider the sequence of functions $\{\neg F_N(V)\}_{N=1}^{\infty}$ it clearly approaches the piece wise function

$$\lim_{N\to\infty} \neg F_N(V) = \begin{cases} 0 & V < 1 \\ 1 & V = 1 \end{cases} \tag{16}$$

See Proof 1 in appendix A

I use the graphs to the left to consider by inspection which approximation behaves the most like our recursive function. First, consider the case where P_N decreases with increased group size. In Fig. 1 the dashed curves, showing the approximation in equation 15 do not change much at all with increased group size. When we compare it to the recursive formulation, we see that the recursive solution changes drastically with increased group size.This tells us that having P_N decrease with increased group size does not capture the increasing marginal cost of foraging time well enough.

If instead we use a constant P_N as in equation 13, we see in Fig. 2 that the approximation still does not change much with group size whereas the recursive solution changes drastically. This tells us that having P_N constant does not capture the increasing marginal cost of foraging time well enough, although it is marginally better than the decreasing P_N solution.

The closest simple approximation to the recursive solution is the approximation wherein P_N increases with N. Using increasing P_N as in equation 14 is the first approximation that represents the behavior of the recursive solution well enough. Importantly we see in Fig. 3 an increasingly steep slope close to $V = 1$ and a decreasing slope at low V. While our approximation begins to deviate the recursive solution increasingly for greater N, it captures the idea of increasing marginal cost for V.

To finish the formulation of μ, note that the likelihood of being killed can be restated as the likelihood of not fleeing given the presence of a predator. So to complete the approximation with an appropriate

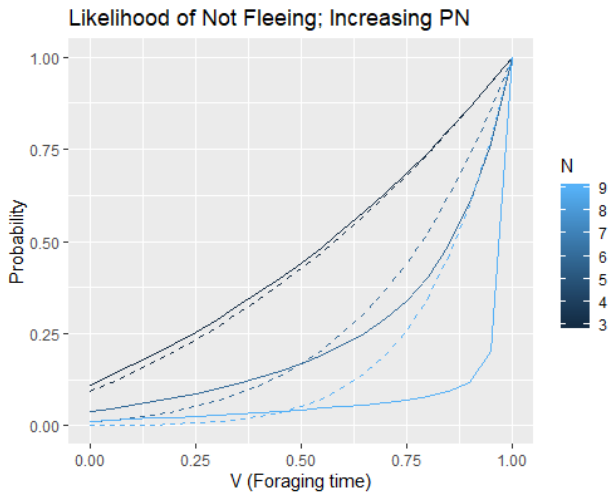


Figure 3 Shows the approximation where P_N is increasing with group size (Eq. 14) Dashed lines are the approximation, solid lines are the recursive solution.

expression for the risk that any one individual is attacked, $P_A(N)$.

It is well understood that as group size increases there is a dilution of predation risk for an individual (Taylor 1976, Turner 1985). It is also well understood that increased group size leads to increased visibility to predators (Taylor 1979, Ioannou 2007). Because there is so much variability in predator strategy and group foraging behavior there is not an obvious way for formulate $P_A(N)$. For this model I consider the dilution effect of group size to go as $1/N$, although position of an individual is important in determining P_A, with no spatial information in the model I consider only the average affect of dilution which is $1/N$.

Now suppose a group is foraging in circle, as N grows, then $A = \pi r^2 \propto N$, so $r \propto \sqrt{N}$. It is reasonable to imagine that, if a predator is hunting at the same elevation as the prey is foraging, the likelihood that a predator notices a particular group is proportional to the radius of space the group takes up which is proportional to N. That is to say that increased risk of being noticed as a group grows as $\sqrt{N}$. Thus I formulate the probability of being attacked in a group of size N as:

$$P_A(N) = \frac{P_0}{\sqrt{N}}$$

where P_0 is the likelihood that a predator attacks an individual that is alone.

This completes our formulation for μ which is

$$\mu = (1-(1-V)P_v)\left(1-(1-V)\frac{N}{C+N}P_V\right)^{N-1}\frac{P_0}{\sqrt{N}} \tag{17}$$

Now that both α and μ formulated in terms of V and N, I can put them together to produce a reasonable expression for fitness.

The Model

In a group of size N, in which every individual is using the same foraging strategy, V, the fitness of any individual is

$$w(V,N) = \frac{s_0 V\sqrt{N}}{(1+aV)^{N-1}(1+s_2V)(1-(1-V)P_v)(1-\frac{(1-V)NP_v}{C+N})^{N-1}} \tag{18}$$

In order to do pairwise invasion analysis, however, we consider a group wherein one mutant individual plays a separate strategy, u. This perturbation gives us a different fitness for the resident and the mutant.

Resident and mutant fitnesses are described as

$$\begin{aligned} w_r(u,V,N) &= \frac{s_0 V\sqrt{N}}{(1+aV)^{N-2}(1+au)(1+s_2V)(1-(1-V)P_v)\left(1-\frac{(1-V)NP_v}{C+N}\right)^{N-2}\left(1-\frac{(1-u)NP_v}{C+N}\right)} \\ w_m(u,V,N) &= \frac{s_0 u\sqrt{N}}{(1+aV)^{N-1}(1+s_2u)(1-(1-u)P_v)\left(1-\frac{(1-V)NP_v}{C+N}\right)^{N-1}} \end{aligned} \tag{19}$$

With these two fitnesses we can determine a fitness differential between mutant and resident. When resident fitness is greater than mutant fitness the resident strategy will hold but when mutant fitness is greater than resident fitness the mutant strategy will invade. I call this fitness differential $\Delta\tilde{w}(u,V,N)$ and which formulated as $w_r(u,V,N) - w_m(u,V,N)$ thus when $\Delta\tilde{w}(u,V,N) > 0$ the mutant can not invade the resident group. factoring out like terms and calling that K_0 we find that

$$\begin{aligned} \frac{\Delta\tilde{w}(u,V,N)}{K_0} = &\frac{V}{(1-au)(1-s_2V)(1-(1-V)P_v)\left(1-\frac{(1-u)NP_v}{C+N}\right)} - \\ &\frac{u}{(1-aV)(1-s_2u)(1-(1-u)P_v)\left(1-\frac{(1-V)NP_v}{C+N}\right)} \end{aligned} \tag{20}$$

The magnitude of the fitness differential does not matter for our analysis because we are not interested in the speed of fixation so we will discuss $\Delta w(u,V,N) = \frac{\Delta\tilde{w}(u,V,N)}{K_0}$ It is still true that when $\Delta w(u,V,N) > 0$ the resident strategy, V resists invasion from the mutant strategy u.

$$\begin{aligned} \Delta w(u,V,N) = &V(1-aV)(1-s_2u)(1-(1-u)P_v)\left(1-\frac{(1-V)NP_v}{C+N}\right) \\ &- u(1-au)(1-s_2V)(1-(1-V)P_v)\left(1-\frac{(1-u)NP_v}{C+N}\right) \end{aligned} \tag{21}$$

We can now consider pairwise invasion analysis of $\Delta w(u,V,N)$ I plot the surface defined by $\Delta w : [0,1]\times[0,1] \to \mathbb{R}$ for constant N. Wherever this surface is positive, the resident strategy resists invasion. From this I can produce a pairwise invasibility plot (Diekmann 2004) wherein the regions where the resident strategy resists invasion are shaded.

Two examples of Pairwise Invasion Plots (PIPs) are pictured below. These PIPs tell us a lot about the system visually. Groups always start along the line $u = V$ because there are no mutants. Upon innovation, the group moves, on the plot, away from the line $u = V$ in the u direction. If the region into which the group moves is not shaded then the mutant strategy will invade and the group will move in the V direction on the plot until it returns to the line $u = V$ meaning that the mutant strategy has become the new resident strategy. If the region is shaded then the mutant strategy does not invade and the group moved back to its original position. We can think of behavioral evolution, then, as movement along the line $u = V$. When the region above the line is not shaded groups will move in the positive direction and when the region above the line is shaded groups will move in the negative direction. This means that the point in right in Fig. 4 where the shaded region crosses over the line $u = V$ is a stable equilibrium and the point on the left in Fig. 4, closer to the point (1,1) is an unstable fixed point. In both cases the stable equilibrium

represents an Evolutionary Stable Strategy (ESS), which is a strategy which no nearby mutant can invade (Smith 1982). This can be seen as a vertical linear neighborhood about the singular point on the PIP which lies totally in the region wherein the residents resist invasion(Geritz et al. 1998). More powerfully, these two stable fixed points are also Convergent Stable Strategies (CSS), meaning that there exists a neighborhood about this singular point for which an individual closer to the fixed point would be able to invade a group of residents further from the fixed point. (Christiansen 1991) The unstable fixed point is not an ESS nor a CSS. It is an evolutionary repeller where there exists a neighborhood wherein a mutant farther from the singular strategy can always invade a group of residents closer to the singular point. This means that a group near that singular strategy will always move away from it.

Any line or curve along which $\Delta w(u, V) = 0$ is shown as a boundary of the shaded region in this plot. These boundary curves are called isoclines. A group will stay on an isocline in the absence of innovation because neither the mutant nor resident have a fitness advantage. In all cases there is an isocline, which I call $\mathcal{I}_1$, along the line $u = V$ because when mutant and resident use the same strategy the fitness differential is necessarily zero. The other isocline, $\mathcal{I}_2$, is complicated but found easily. Because $\Delta w(u, V)$ is a polynomial, and $u = V$ is always a solution, the other solution can be found simply by finding where the surface $\mathcal{S}(u, V)$ crosses the u, v plane. Where

$$\mathcal{S}(u, V) = \frac{\Delta w(u, V)}{(V - u)} \tag{22}$$

Furthermore, $\mathcal{S}$ is necessarily a polynomial in u and V by the factorization theorem. This means that the second isocline, $\mathcal{I}_2$, can be described by

$$\mathcal{I}_2 = \{(u, V) \in [0, 1] \times [0, 1]; \mathcal{S}(u, V) = 0\} \tag{23}$$

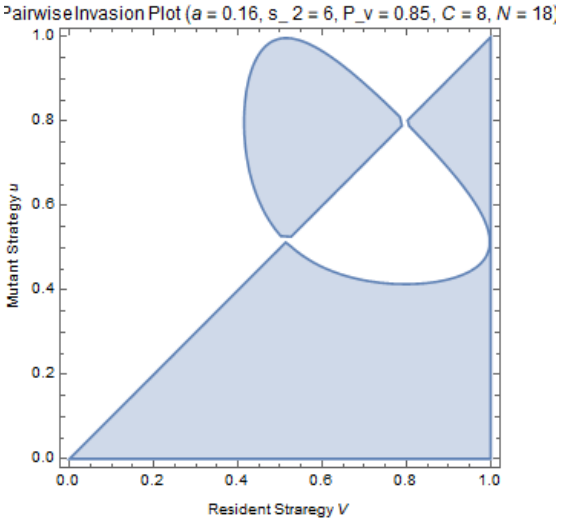


Figure 4 A pairwise invasibility plot for the parameters $a = 0.16, s_2 = 6, P_v 0.8, C = 86, N = 18$ Shaded regions show where the resident strategy resists invasion.

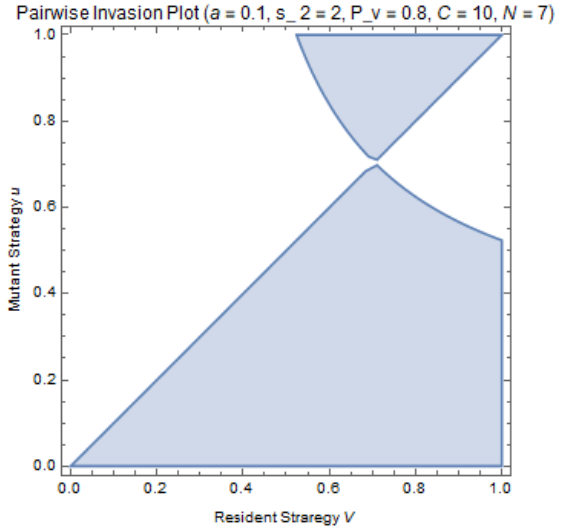


Figure 5 A pairwise invasibility plot for the parameters $a = 0.1, s_2 = 2, P_v 0.8, C = 10, N = 7$ Shaded regions show where the resident strategy resists invasion.

An important note is that we constructed $\mathcal{S}$ by dividing by $(V - u)$ so that it is positive when the shaded region is below the line $u = V$ and negative in the opposite case. In the above discussion I noted that behavioral evolution can be thought of as motion along the line $u = V$ so now consider $\mathcal{S}$ constrained to the line $u = V$, which will be a polynomial in V. I call the polynomial $\mathcal{P}(V)$.

$$\begin{aligned}\mathcal{P}(V) = &- C(-1 + P_v + P_v s_2 V^2 + a P_v(2V + (-1 + s)V^2) - a(2V + s_2 V^2)) + \\ &N(1 + P_v(-1 + V))^2(1 + a(2V + sV^2))\end{aligned} \tag{24}$$

Which is more usefully written as the 4th degree polynomial in V

$$\begin{aligned}\mathcal{P}_4(V) =& C + N - CP_v - 2NP_v + NP_v^2 + (2aC + 2aN - 2aCP_v + 2NP_v - 4aNP_v - 2NP_v^2 + 2aNP_v^2)V + \\ & (aCP_v + 4aNP_v + NP_v^2 - 4aNP_v^2 + aCs_2 + aNs_2 - CP_vs_2 - aCP_vs_2 - 2aNP_vs_2 + aNP_v^2s_2)V^2 + \\ & (2aNP_v^2 + 2aNP_vs_2 - 2aNP_v^2s_2)V^3 + (aNP_v^2s_2)V^4\end{aligned} \tag{25}$$

Thus, when they exist, the roots on the interval $[0, 1]$ of the above polynomial are parts of $\mathcal{I}_2$. Furthermore, because they are necessarily on the line $u = V$ they are also on $\mathcal{I}_1$ and are thus fixed points.

Now, recall that groups move in the positive V direction along the line $u = V$ when the region above the line $u - V$ is not shaded and $\mathcal{S}(u, V) > 0$ is this case. Thus I use $\mathcal{P}_4(V)$ as an expression for the direction of movement of a group in terms of V. Importantly, the magnitude of $\mathcal{P}(V)$ is not important, only the sign. The magnitude of $\mathcal{P}(V)$ tells us only how quickly small innovations close to V become fixed which is unrelated to how often innovations arise. Let ε be thought of as the average magnitude of innovation; it will determines how far along the V axis a group moves in one time step. Later we will consider the affects of having ε represent an innovation rate which is close to the rate of change in group size, but first we find equilibria with a very slow innovation rate and constant innovation magnitude. Note that ε is very small and independent of V and N.

Thus we have the following differential equation

$$\frac{dV}{dt} = \varepsilon \text{sign}(\mathcal{P}(V)) \tag{26}$$

At this point, with constant group size, the model shows several interesting trends. Particularly of note is vigilance's change with respect to group size. Below I show two bifurcation diagrams of vigilance with a as the bifurcation parameter. The most important finding at this point is that at a constant group size vigilance decreases with increased competition. This will be important in the discussion of dynamic group size. This may be intuitive because when competition is high, a mutant playing a high foraging, low vigilance, strategy will impose a greater fitness determent to its group mates and will thus be more likely to invade than it would be in a low competition environment. This result changes when group size can change.

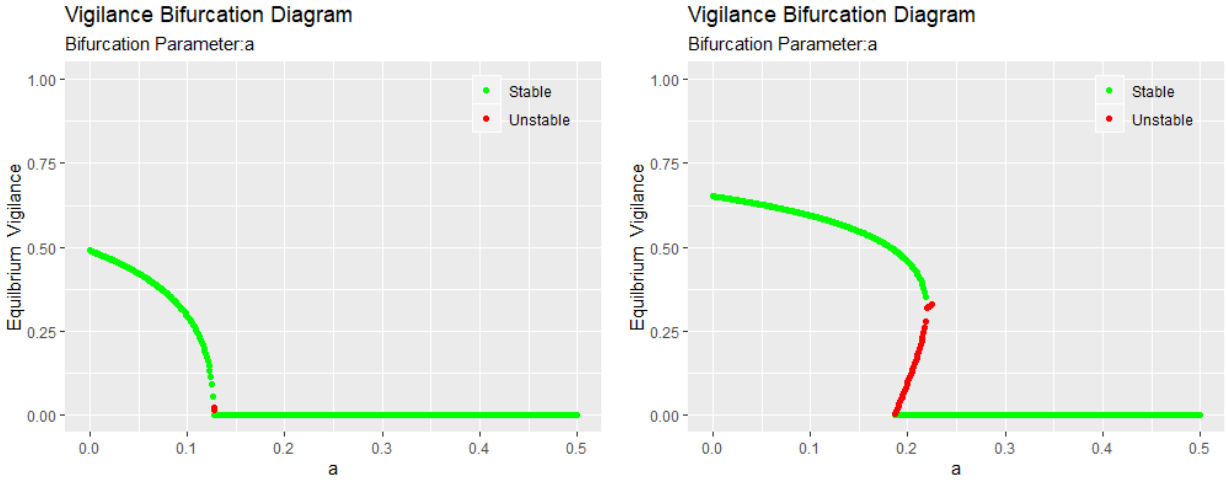


Figure 6 Left is a bifurcation diagram showing the fixed points of E which is $1 - V$ when P_v=0.8. on the **Right** is another Bifurcation Diagram with with a prominent saddle node bifurcation when $P_v = 0.68$

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Group Size

Recall that $\mathcal{P}(V)$ depends on N and N will be dynamic in our system so we can describe the change in V through time as

$$\frac{dV}{dt} = \varepsilon \text{sign}(\mathcal{P}(V, N)) \tag{27}$$

Group size is dynamic and dependent on vigilance. There are two ways in which group size may be determined. When individuals can leave and join a group whenever they like, I call this external control. When group size is determined by individuals within the group it is called internal control. We first consider external control.

When individuals can join a group freely, they will do so selfishly, whenever they can increase their fitness by joining a group. This means that when fitness of an average individual in a group of size N is greater than the fitness of a single individual, the group will grow until the fitness of the average individual in the group is the same as the fitness of a single individual. This is called the "stable group size." (Giraldeau 1988) Thus we can say that group size will change as proportionally to the fitness differential $w(V, N) - w(V, 1)$

$$w(V, N) - w(V, 1) = \frac{s_0 V}{(a + s_2 V)(1 - (1 - V)P_v)} \left(\frac{\sqrt{N}}{(1 + aV)^{N-1} \left(1 - \frac{(1-V)NP_v}{C+N}\right)^{N-1}} - 1 \right) \tag{28}$$

By finding a common denominator it becomes clear that group size will grow as

$$\frac{dN}{dt} = \sqrt{N} - \left((1 + aV) \left(1 - \frac{(1 - V)NP_v}{C + N} \right) \right)^{(N-1)} \tag{29}$$

Group size will tend towards the stable fixed point, N_E^*, which I call "External Ideal N." There is always at least one fixed point for group size. One fixed point is always $N = 1$, which is typically unstable but may become stable under certain conditions. Often another fixed point exists which has the opposite stability of $N = 1$. N_E^* must be found numerically.

When control of group size is held by members of the group, the group will tend to be the size which maximizes the average fitness of average group member. This is called "optimal group size" and has been shown to be an unrealistic expectation (Sibyl 1983) but it gives us a lower bound for group size (which is discussed later and explained in Proof 4 in appendix A).

Equilibrium group size in this case, N_I^* "Internal Ideal N", can be solved as

$$N_I^* = \arg\max_{n \in \mathbb{Z}} w_r(V, N) \tag{30}$$

More to the point, group size will increase when fitness increases with group size and decrease in the opposite case. This means that for a group with total internal control, group size will grow according to the partial derivative of w with respect to N.

$$\text{Sign}\left(\frac{dN}{dt}\right) = \text{Sign}\left(\frac{\partial}{\partial N} w(V, N)\right) \tag{31}$$

The differentiation is included in appendix A as Proof 2. The result can be expressed as

$$\frac{dN}{dt} = 1 + 2N\left(-\log\left(\xi(N)\right) + (1-N)\frac{\xi'(N)}{\xi(N)}\right) \tag{32}$$

where $\xi(N) = (1+aV)\left(1 - \frac{(1-V)P_v N}{C+N}\right)$. By inspection we can see that there is either 1 or 0 solutions to $\frac{dN}{dt} = 0$ which, when it exists, is stable. It has no analytical solution, so it must be found numerically.

So to summarize we have two similar systems for vigilance and group size.

External Control System

$$\begin{aligned}\frac{dN}{dt} &= \sqrt{N} - \left((1+aV)\left(1 - \frac{(1-V)NP_v}{C+N}\right)\right)^{(N-1)} \\ \frac{dV}{dt} &= \varepsilon(\text{sign}(\mathcal{P}_4(V,N)))\end{aligned} \tag{33}$$

Internal Control System

$$\begin{aligned}\frac{dN}{dt} &= 1 + 2N\left(-\log\left(\xi(N)\right) + (1-N)\frac{\xi'(N)}{\xi(N)}\right) \\ \frac{dV}{dt} &= \varepsilon(\text{sign}(\mathcal{P}_4(V,N)))\end{aligned} \tag{34}$$

Note that in these systems $\varepsilon \ll a, C, s_2, P_v, V, N$, because V changes very slowly relative to N

Numerical Analysis

Finding fixed points is just a matter of finding zeros in the above systems (eq.33 and eq.34). There are several issues, however, with reporting only fixed points. The first is the boundary conditions of vigilance. Vigilance is restricted to $[0, 1]$. These bounds, which are not represented in $\mathcal{P}_4(V)$, mean that some solutions find their equilibria along a boundary instead of a zero of the system. Secondly, most fixed point in the system are unstable. pictured below are figures showing all fixed points for solutions in the parameter space $\{(a, s_2, P_v, C) \in (0, 0.5) \times (0, 10) \times (0, 1) \times (0, 20)\}$ on the left, and only stable fixed points on the right.

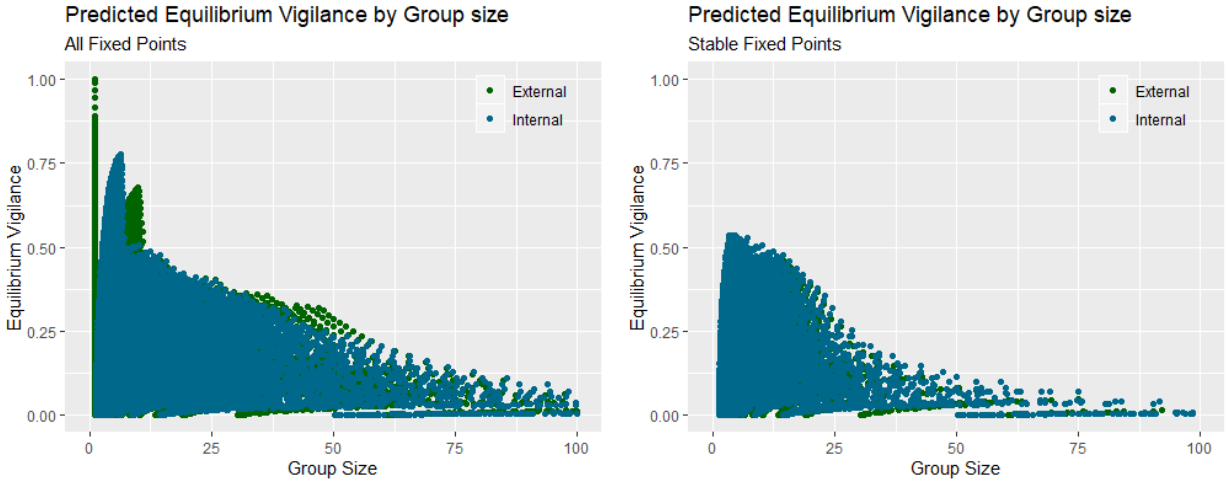

Figure 7 Left all fixed points in both internal and external systems. **Right** and all Stable fixed points in both internal and external systems from the parameter space $\{(a, s_2, P_v, C) \in (0, 0.5) \times (0, 10) \times (0, 1) \times (0, 20)\}$. There are 42000 fixed points on the left (an internal and external fixed point for each point tested in the parameter space) and only 11505 of those are stable pictured on the right.

The presence of so many unstable fixed points seems to imply a great number of solutions escaping to infinity but this is not the case. It is easy to prove that no solutions escape to infinity. The Proof is Proof 3 in appendix A.

Thus we know solutions either approach a stable equilibrium, or find a stable cycle. So, to fully address overall trends found in the model, I examine solutions instead of simply examining fixed points.

Because N changes quickly while equilibrium vigilance ($E = 1 - V$) changes slowly, finding a stable attractor, whether it is a point, (N, E), or a cycle, requires us to trace the solution in a non standard way. The algorithm begins with an initial vigilance level, solving for group size, then adjusting vigilance, and repeating the process until neither vigilance nor group size changes significantly between iterations. Solving this as a typical dynamical system, which is further discussed later, would suppose that vigilance can change with a rate comparable to the rate of change in group size.

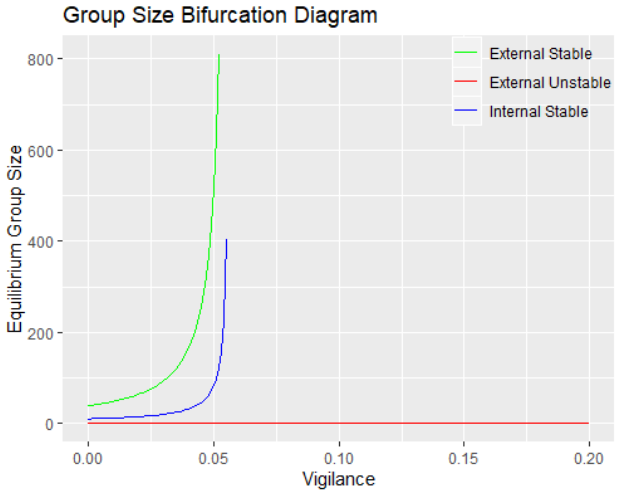

Figure 8 A bifurcation diagram of group size when competition is low ($a = 0.05$)

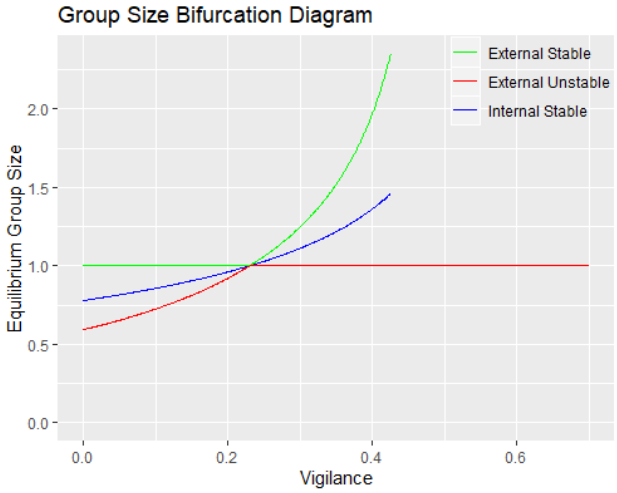

Figure 9 A bifurcation diagram of group size when competition is high ($a = 0.9$)

In this method, we first find equilibrium N for some set of parameters and some initial vigilance. Next it is determined if a strategy of greater vigilance or less vigilance can invade by checking $\text{sign}(\mathcal{P}_4(V, N))$. If it is positive, strategies with less vigilance (higher V) will invade so V will increase. If it is negative, Vigilance will decrease.

This process can be though of as movement along a bifurcation curve of group size. From any initial condition, group size immediately conforms to its stable equilibrium then as vigilance increases or decreases incrementally, group size corrects at each increment. For this reason it is helpful to see the bifurcation diagrams for N_E^* and N_I^*.

Bifurcation diagrams for both internal and external ideal group size are pictured in Figs. 7 and 8. Notice that the diagrams are actually picturing two different systems. The External system (in red and green) has two curves of fixed points. When competition is low (Fig. 8) these curves of fixed points never meet. A group size of 1 is always unstable and a larger group size is always stable. When competition is high (Fig. 9) the dynamics are different. At very low vigilance group size is stable at one, however, there is a transcritical bifurcation, where, after vigilance has increased a certain amount, stable group size increases above 1. Even in this case, however, there is only ever 1 or zero stable fixed points.

The Internal System (in blue) is a little simpler because there is never more than one fixed point in the system and that fixed point is always stable. This means that the internal system also exhibits monostability. An important observation about these two systems is that internally controlled

group size is always less than externally controlled group size. Even more powerfully we can say that Internal Ideal group size is between the stable and unstable manifolds in the externally controlled system. The proof is simple and not important to the model. It is Proof 4 in Appendix A.

Solutions will travel along these bifurcation curves because vigilance changes very slowly compared to group size. Below I show several solutions as they first conform to the curve of fixed points then travel along it until they reach equilibrium.

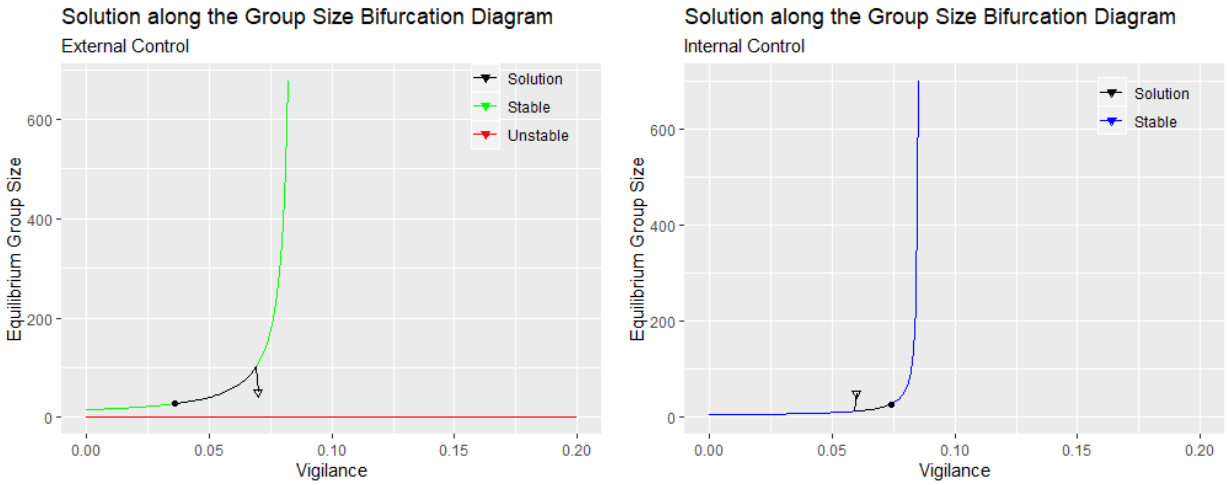

Figure 10 Solutions using parameters $a = 0.1, s_2 = 10, P_v - 0.9, C = 6$ with initial conditions $V = 0.93, N = 50$ for both the **Left** External Control System and **Right** Internal Control System. The open triangle is the initial condition and the closed circle is the equilibrium.

This may appear to suggest that group size increases with vigilance but that is incorrect. Equilibrium Group Size increases with constant vigilance but vigilance is dependent on N. Thus, in order to examine the relationship I find many equilibria for many different sets of parameters. Because group size never exhibits bistability, there is only one stable attractor for a set of parameters. This means that no matter the initial condition, every solution will tend towards that fixed point. Thus in order investigate our entire parameter space we need not vary our initial condition, only each of the 4 parameters in their reasonable interval.

Results

By varying a on the interval $[0.01, 0.5]$, P_v on the interval $[0.05, 1]$, s_2 on the interval $[1, 10]$, and C on the interval $[2, 20]$ I show the space where the stable attractors are in on the Vigilance×Group Size plane (Fig. 11). The key thing to notice is that with higher equilibrium group size, the upper limit of equilibrium vigilance decreases. This fits the well observed relationship between group size and vigilance. It also makes sense logically; for large groups, the cost of not being vigilant, which is the risk of death while foraging, is far less and thus it is unreasonable to expect a large group to exhibit high amounts of vigilance. This gives further mathematical support to the nature of the relationship from a game theory perspective. It is also of note that the frontier of the equilibria for the external control system is farther from (0,0) than the internal control system. This is supported by the fact that Internal Ideal N is always less than External Ideal N. The two distributions are also pictured separately below (Fig. 12).

The model output was visualized by simply finding the equilibrium solution for each set of parameters in a reasonable parameter space. Because the technology available limited how small ε could be, there were

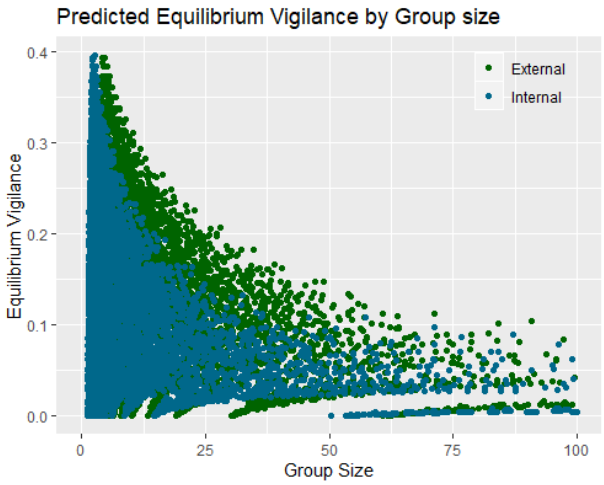

Figure 11 Shows a low resolution image of the space wherein there is a stable attractor for this system.

some numerical errors like solutions seeming to escape to infinity. Recall that this is impossible as discussed earlier. We see that this is related to the limit cycles discussed before. For certain sets of parameters, group size is extremely sensitive to vigilance. When vigilance increases, it becomes always beneficial for an individual to join a group or for a group to take in an individual so ideal group size grows to infinity. This increase of group size selects for low vigilance strategies and vigilance falls again. In some cases this may be a stable spiral eventually finding a fixed point. In other situations this results in a stable limit cycle around an unstable spiral. This is discussed in more detail later. For certain sets of parameters the process of finding such a stable attractor, involves many more iterations than is reasonable given available computing resources. Removing erroneously found solutions escaping to infinity, we are left with the pictured distributions which represent the space where this model predicts groups may lay in the group size×vigilance plane.

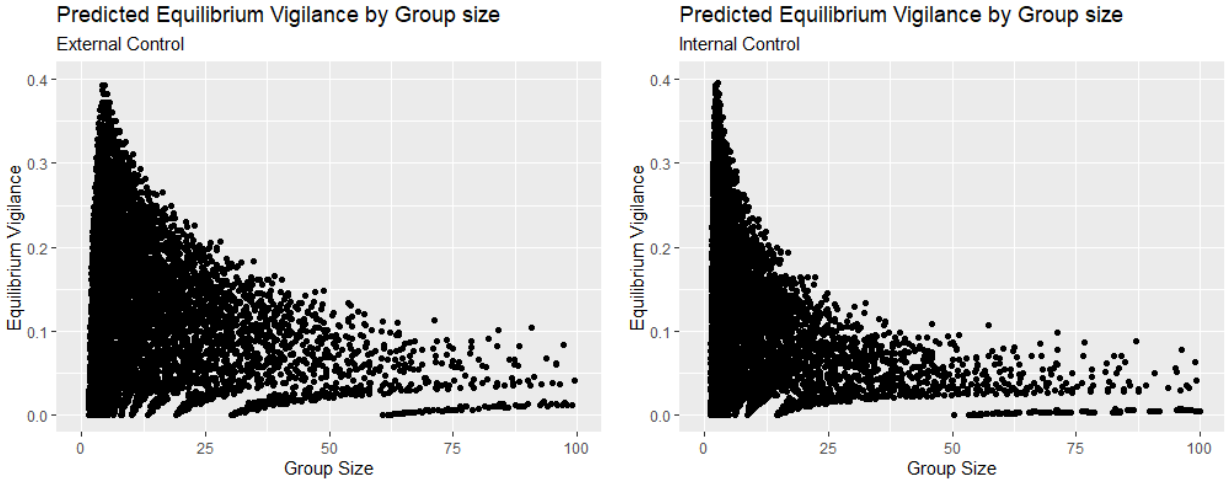

Figure 12 low resolution images of the space wherein there are equilibria for a some choice of parameters for **Left** the external control system and **right** the internal control system.

Both systems exhibit the same general shape and the same conclusion about the frontier of group size and vigilance. It is important to note that these figures do not show density. There are many more equilibria close to $N = 1$ than there are at large N. These figures only show the region wherein there may be equilibria. Use of regression on the model output would be better suited to display information about density of equilibria.

Below is also pictured the variation in parameter values for all of the equilibria for both systems separately. Examining this allows us to get a better understanding of how certain parameters impact the vigilance-group size relationship. The only parameter which shows a easily discernible trend is the intensity of competition, a. The trend shown is that high competition results in high vigilance small group size

strategies while low competition results in low vigilance and high group size. The relationship is mostly unsurprising because competition has such powerful control over group size. When competition is very high, we see that group size is limited but when competition is low groups can grow much larger and as a result vigilance is more limited. The part that is surprising is competition's effect on vigilance. With higher competition we might expect that more time needs to be devoted to foraging to get a similar benefit so equilibrium vigilance would be lower, as was the case with static group size (Recall Fig 6). This is interestingly not the case and is explored further later. While trends in other variables are hard to discern from the below figures, it can be shown by varying only one parameter and holding the others constant, that competition is the only parameter whose variation results in a negative relationship between group size and vigilance. Variation in all other parameters results in a positive relationship between the two, contrary to the well observed trend.

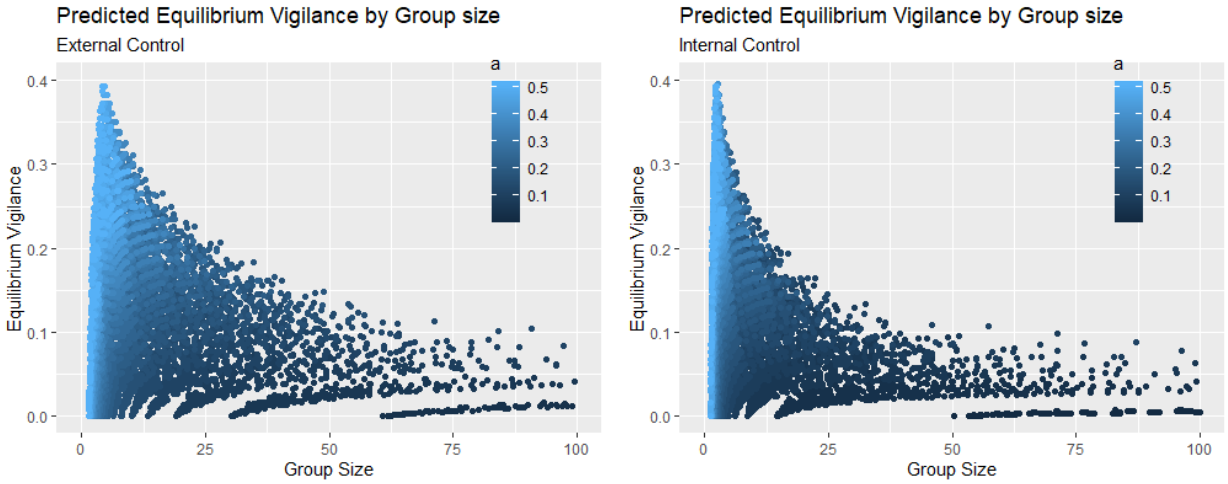

Figure 13 Equilibrium position resulting from varying all four parameters for both the **left** external control system and **right** the internal control system Displayed by color is intensity of competition (a)

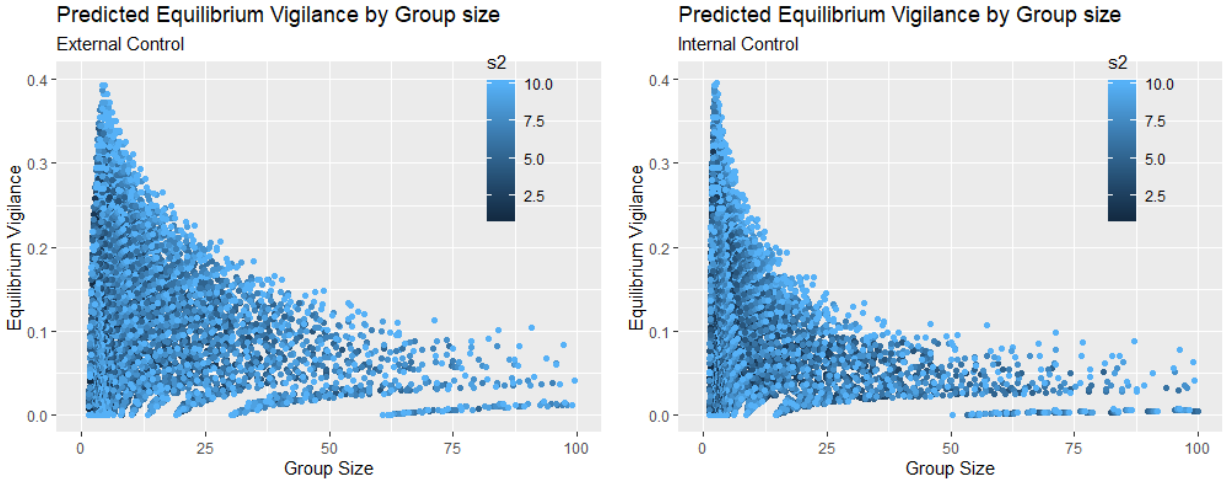

Figure 14 Equilibrium position resulting from varying all four parameters for both the **left** external control system and **right** the internal control system. Displayed by color is food handling time (s_2)

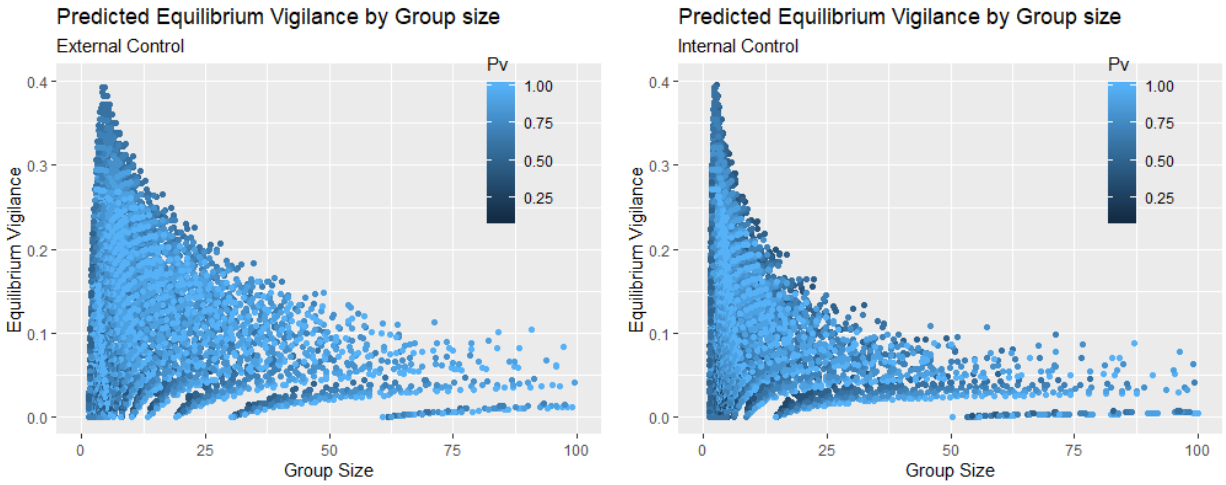

Figure 15 Equilibrium position resulting from varying all four parameters for both the **left** external control system and **right** the internal control system. Displayed by color is the likelihood of seeing a predator (P_v)

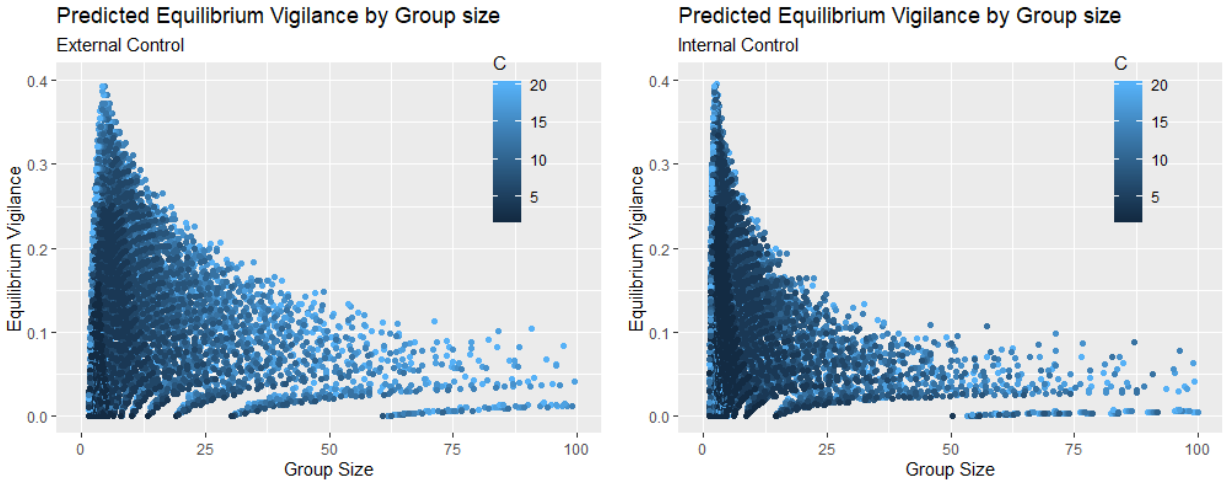

Figure 16 Equilibrium position resulting from varying all four parameters for both the **left** external control system and **right** the internal control system. Displayed by color is the parameter C which is inversely proportional to the transmission of antipredator information. in very light areas the likelihood that one individual receives antipredator information from another individual is low relative to the dark regions.

To better understand the relationship between competition, group size, and vigilance, I fix all other parameters and vary competition over the same range with greater resolution. This reveals several things about the model output. First it is a reminder that the reason the space on the bottom of the figures above are empty is because of poor resolution. In reality stable attractors occupy that space, but because the resolution used in finding the space was too low the low density of solutions in that space meant that few were found numerically. Secondly it shows how competition drives the relationship between group size and vigilance. For a particular choice of the other three parameters, equilibria were found by varying a. The results are pictured below on the group size$\times$vigilance plane (Fig. 17) and with both group size and vigilance as a function of competition (Fig. 18).

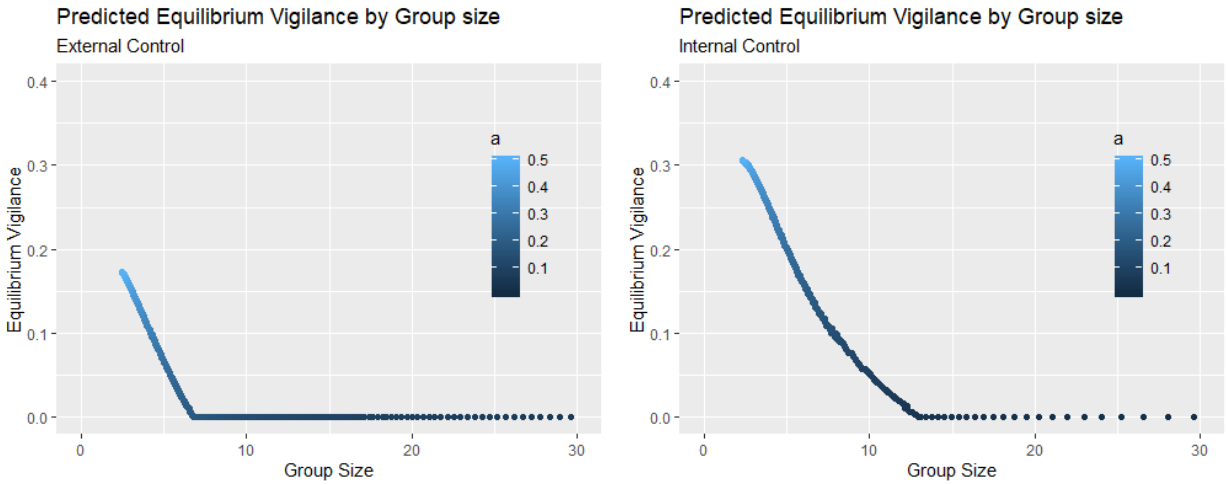

Figure 17 Equilibrium position resulting from varying only intensity of competition (a) for both **left** external control system and **right** the internal control system. Here $s_2 = 4, P_v = 0.75, C = 6$

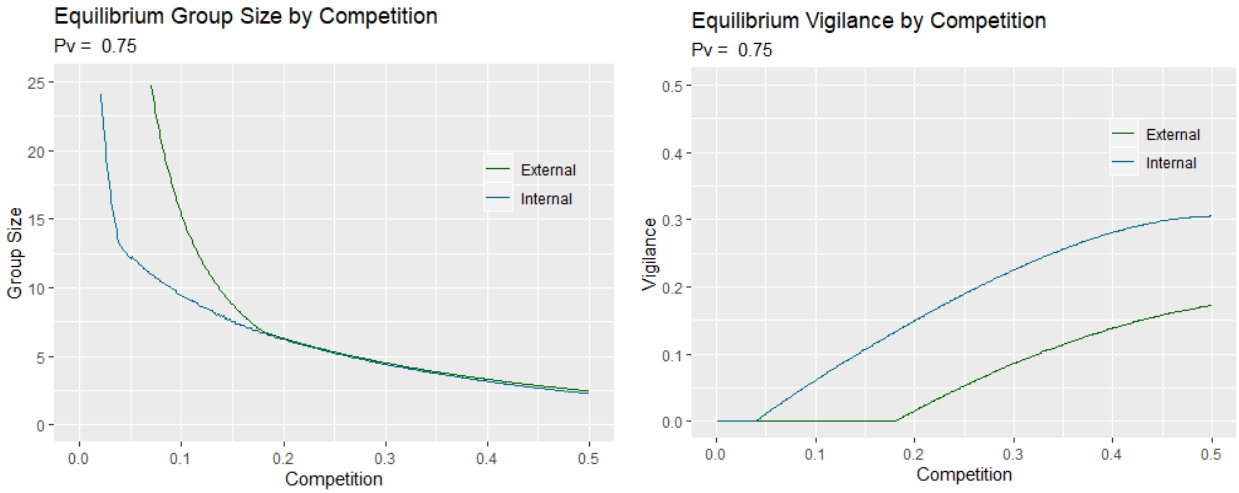

Figure 18 Left Equilibrium group size as a function of competition and **Right** Equilibrium vigilance as a function of competition in the parameter space $(a, s_2 = 4, P_v = 0.75, C = 6)$

These figures predict the observed negative relationship between group size and vigilance and will be discussed further later. In this parameter space $(a, s_2 = 4, P_v = 0.75, C = 6)$ group size and vigilance form nice smooth curves as function of competition. With sufficiently small ε the same would be true for any parameter space. However, ε is limited by computing power, so there are cases in which it appears, using this process of finding stable fixed points, that solutions are not continuous with respect to competition, which gives the curve of fixed points a jagged appearance (Fig. 19). This seems to only occur in the internal control system, however. Internal Ideal N is more sensitive to changes in vigilance than External Ideal N which means that a larger ε produces an "over shooting" effect (discussed in more detail later) more easily in the internal control system. We cannot offer a biological interpretation for the increased sensitivity to vigilance in the internal control system, it may be an area of further study.

Other Approaches

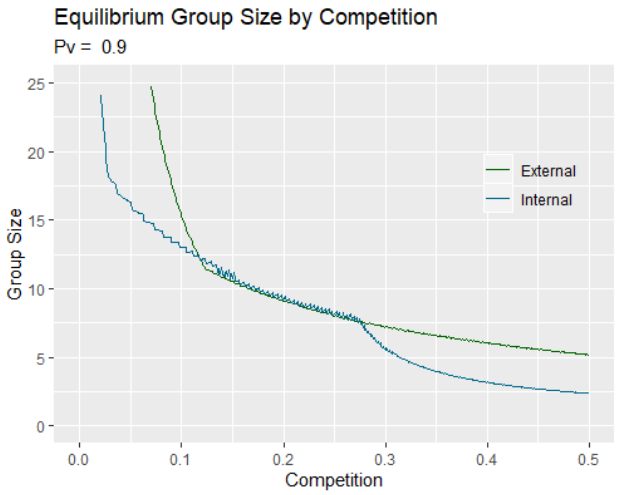

Figure 19 Shows equilibrium group size found with constant innovation magnitude as a function of competition.

The above results are important but can be obscures as a byproduct of the constant magnitude of innovation. When ε is too big, it results in the solution "over shooting" it equilibrium and, when ε is constant, this introduces two-cycles which obscure the model results when groups size is very sensitive to a change in vigilance. Because of limitations in available computing power there is a lower limit on ε. An example of the affect of constant magnitude of innovation is shown in Fig. 19. Whereas equilibrium group size as a function of competition formed a smooth curve in Fig. 18 when $P_v = 0.75$, the function is not smooth at a higher P_v. Zooming in on a single solution gives some explanation for this result.

The bifurcation diagram for vigilance with a solution superimposed explains the seemingly discontinuous feature of group size in this particular region. Because vigilance changes slowly relative to group size the solution does not conform to the bifurcation curve as it does in the group size bifurcation diagram. This figure (Fig. 20) shows that vigilance and group size come to an equilibrium around an unstable fixed point for vigilance with fixed N.

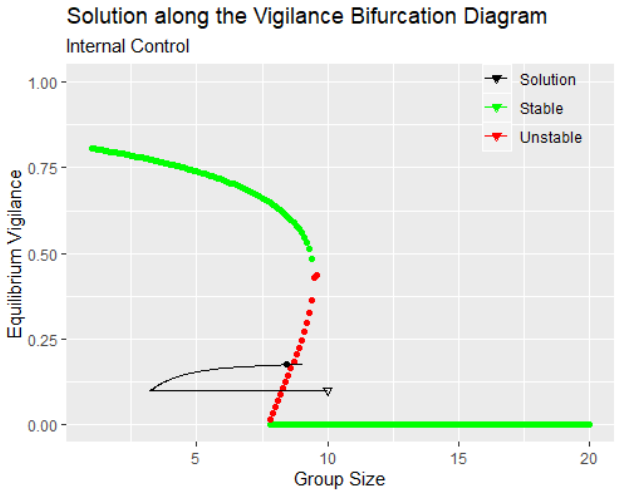

Figure 20 shows a solution with constant innnovation starting at (10,0.1)(shown by the open triangle) on the bifurcation diagram for vigilance.

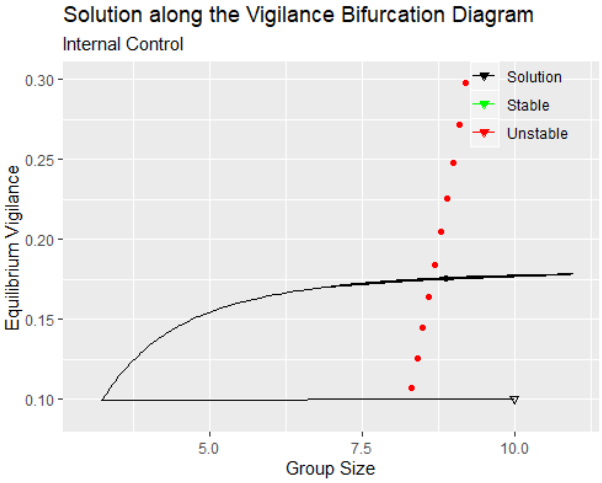

Figure 21 Shows a zoomed in image of the stochastic solution for the same initial condition as above on the bifurcation diagram for vigilance

When a group has a vigilance level above the unstable fixed point (as in Fig. 21) strategies of greater vigilance will invade, but when they do group size will increase in response because, especially for internally controlled groups, members will maximize their fitness by letting more high vigilance individuals into the group.

This increase in group size moves the group on the bifurcation diagram to a point below an unstable fixed point so now strategies of less vigilance will invade. That change in strategy changes the group size again and puts the group back on the other side of the bifurcation curve to repeat the cycle. This constant selection for vigilance strategies other than the equilibrium strategy means that vigilance is constantly changing.

For both external and internal control systems this causes a change in group size. Internal control systems are more sensitive to changes in vigilance so the variance in group size is more pronounced. This also reveals that in the region of the curve where internal group size seems to drop below external group size. What is actually happening is the same cyclical pattern but group size escapes to infinity then falls back to a reasonable size. This error happens because the system is being solved as if group size changes instantly. This of course is not true and is the reason why the model shows such a biologically unreasonable result in that space. This shows a limitation of the method used to solve the model but not the model itself.

Solving the system as we would a typical dynamical system, shows more insights into periodic solutions. I continue to use the same variation in competition as an example. Solving the system as we would a typical dynamical system violates the assumption that group size changes much faster than vigilance, but we can use this method to better understand solution behavior. When solved in the typical way our expression for the change in V changes. We now consider

$$\frac{dV}{dt} = \varepsilon \mathcal{P}_4(V) \tag{35}$$

where ε now means the rate of innovation, and the speed at which an innovation is fixed has an effect on the solution.

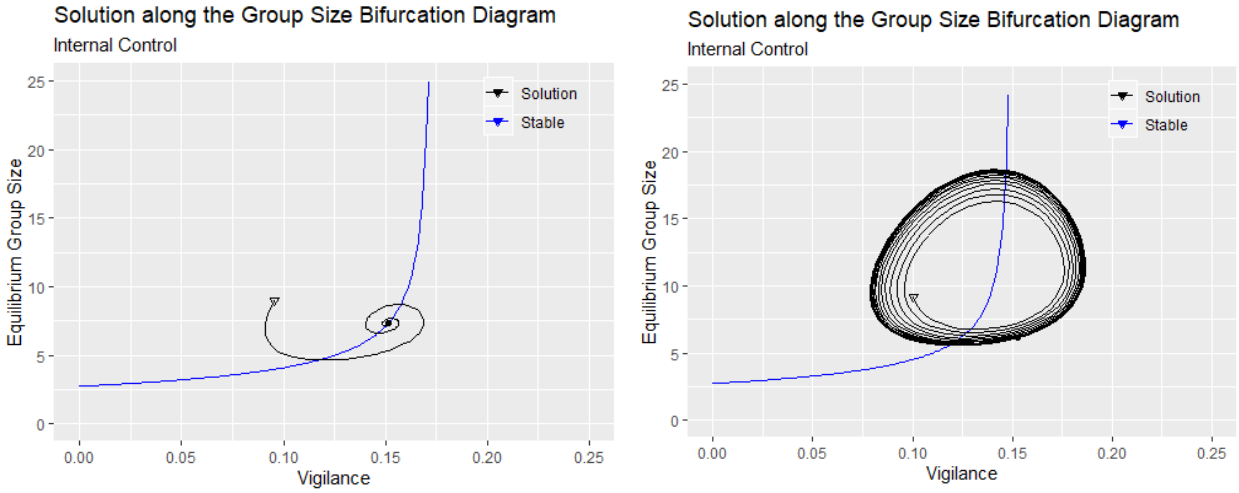

Figure 22 Left Shows a solution solved typically with $a = 0.2, s_2 = 4, P_v = 0.8, C = 6$. **Right** shows a solution solved typically with $a = 0.2, s_2 = 4, P_v = 0.95, C = 6$.

In figure 22 it is clear that solutions do not conform to the bifurcation diagram anymore. This can be thought of as a result of group size changing on the same time scale as vigilance, and it shows under what conditions there are periodic solutions. We see numerically that there are periodic solutions in many cases, especially when a is very high or when P_v is very high. These periodic solutions however have amplitude dependent on ε

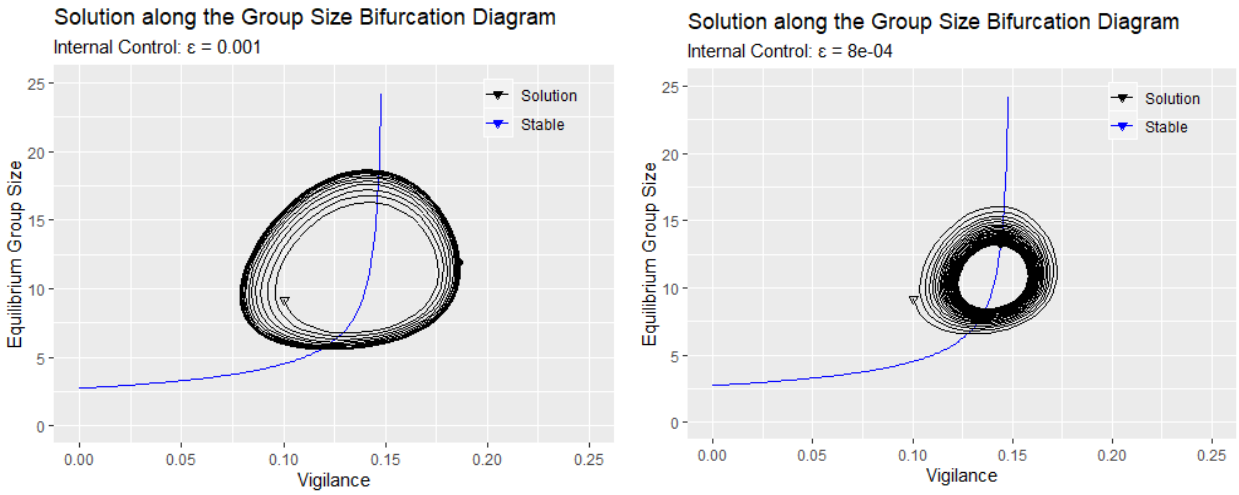

Figure 23 Left Shows a solution solved typically with high ε **Right** shows a solution solved typically with lower ε. Both solutions are from the same set of parameters:$a = 0.2, s_2 = 4, P_v = 0.95, C = 6$

I have shown that periodic solutions are responsible for introducing what is observed as variation in the system. Understanding of how ε affects such solutions tells us that the rate of innovation relative to the rate of change for group size plays a roll in determining the amount of variation. Revisiting variation of competition, figure 24 shows a bifurcation diagram of the internal system with competition as the bifurcation parameter.

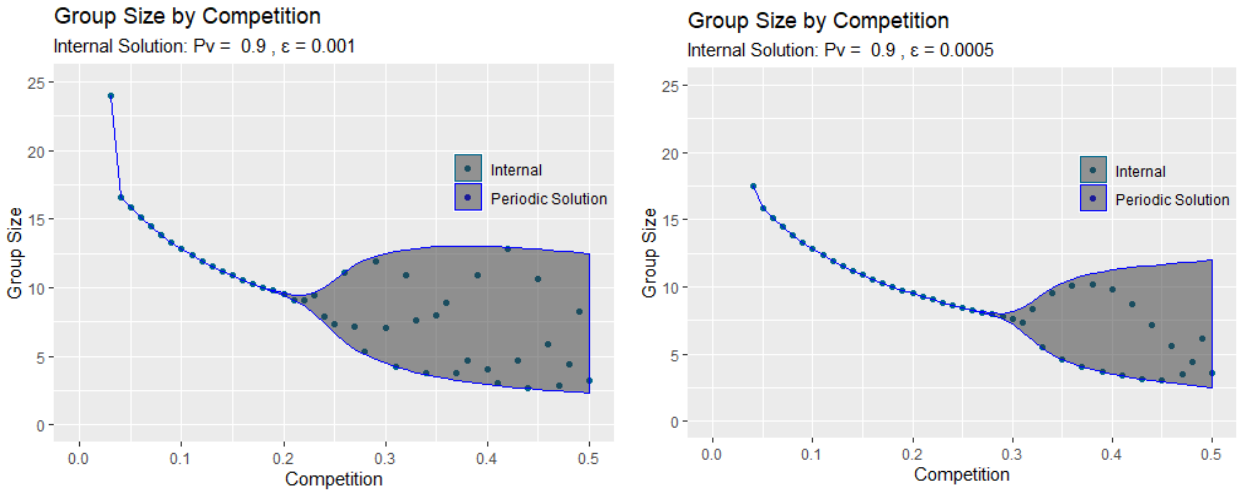

Figure 24 Left shows group size by competition for large ε **Right** shows the same thing with lower ε. Both solutions are from the same set of parameters:$a = as_2 = 4, P_v = 0.9, C = 6$

When ε is high, there is greater amplitude of periodic solutions, when ε decreases amplitude seems to decrease in most of the parameter space. From this we will draw conclusions about how the real system may behave for different speeds of innovation.

Discussion

The goal of producing such a model was to offer an explanation for the emergence of the well observed relationship between group size and vigilance while loosening the requirements for behavioral monitoring and collective detection. The model output shows what factors are important to this emergence. The adaptive mechanism that is described in this model takes place over long periods of time but does not require any individual to know the strategies of any other individual; although, we will discuss the condition when individuals do perceive that information in part. The adaptive dynamic framework shows us how this phenomenon arises naturally through only natural selection and nearly faithful replication. In environments where competition is high, for instance when space for foraging is limited, this immediately limits group size. Whether group size is controlled by current members or potential joiners, high competition restricts the number of individuals in the group. This is not surprising.

What, perhaps, is surprising is the effect that limited group size has on vigilance. A previous model predicted that when group size is variable, high group size would be associated with decreased foraging rate. This result however assumes that an individual can freely move between a large group and a small group of fixed size (Bednekoff and Lima 2004). Allowing group size to change continuously on the integers produces the contrary result which is more consistent with the available data (Elgar 1989) The results of this model show that vigilance increases when competition increases. We know that this is not a result of competition alone because, in the case with fixed group size, increased competition lead to decreased equilibrium vigilance. Thus, the relationship, though it is driven by competition, depends on group size. When there is low competition and thus high group size, strategies of lower vigilance are able to invade because of reduced risk that results from dilution and from being able to observe and respond to another individual's flee response. Importantly, it is not assumed that every individual definitely perceives another individuals flee response, thus we avoid the requirement for total collective detection. This poses interesting questions about the evolutionary advantages of distress calls which could be a future direction for this work.

When risk of death is low, the cost of not being vigilant decreases, so lower vigilance strategies will tend to invade and become fixed until the benefit from foraging is equal to the cost of not being vigilant. This leads to the case where zero vigilance strategies are evolutionarily stable. Group size can grow large enough and risk becomes so diluted that there is no amount of vigilance worth the time spent not foraging. This case may highlight a flaw in the model which supposes that all vigilance time comes at the cost of foraging. This is not necessarily the case. For instance an individual may need to pause its foraging to chew its food or to move between patches and could then scan for predators without a cost to foraging.

In the other case when group size becomes low, the risk of death becomes much higher for each individual so the cost of not being vigilant increases. In this way higher vigilance strategies invade more frequently.

This stands opposed to the expectation in a group of fixed size, when we consider benefit from foraging as the currency. We would expect that at high group size the benefit from foraging would be lower, so individuals would risk less to forage and be vigilant more. Likewise, when group size is small, benefit from foraging is higher so individuals maximize their fitness by foraging more and being vigilant less. This is what results from the model with constant group size but when group size is allowed to change, as it would in reality, the result is reversed. This is an important result and it may be explicable from the stabilizing effect group size has of foraging benefit. Group size is only large when competition is very low and it is only low when competition is high. The opposite effects from group size and competition stabilizes the benefit from foraging which means that risk has more power in determining vigilance and thus the risk based explanation above describes the behavior.

Thus I have shown that the relationship between group size and vigilance across isolated populations

on long time scales can be explained by the following mechanism. When competition is high, group size decreases, and that decrease in group size produces a favorable environment for increased vigilance strategies to invade. small changes in groups size, in reaction to innovation and fixation of new vigilance strategies, continues until the group reaches the convergent stable strategy. In the opposite case, when competition is very low, group sizes may become high and as a result decreased vigilance strategies can invade. Group size and vigilance adjust incrementally until, again, the group reaches a convergent stable strategy. The vigilance CSS in the high competition case is higher than that of the low competition case because high competition reduces the benefit from feeding per unit time so individuals are less likely to risk not being vigilant for as much time in the high competition case.

Although this model is consistent with observed trends across many taxa, there is little experimental evidence to support the claim that variation of competition is the driving factor behind the relationship. Support for this hypothesis would have to involve a reliable quantification of competition intensity across many taxa on large time scales. Experimental support, which is more feasible on a short time scale, discussed below, would require a controlled adjustment of competition intensity, for instance changing the density of food available, and observing if differences in competition significantly affect group size and vigilance in the way this model predicts.

This mechanism works on time scales where nearly faithful replication of vigilance strategies results in rare innovation followed by fixation. Thus we can only use this mechanism, as described above, as an explanation of the group size, vigilance relationship between isolated populations. To fully apply this mechanism within a group which, during the course of its existence, fluctuates in group size and vigilance, we must slightly amend the notion of innovation and fixation.

Consider the case where, instead of vigilance being fixed and maintained through the entire life of the individual, vigilance is thought of as a meme which is shared and modified as public information. Group foragers necessarily encounter inadvertent social information (Dunchin et al. 2004) which is behavioral information about something like foraging or fleeing which can not be hidden but is not an intentional signal. In this category is public information, cues given by the location and performance of others, which is known to be transmissible through mimicry (Giraldeau 1997). There is reason to believe that transmission of public information is selected for because it allows for an individual to gain the benefit from many more "trials and errors" than if it only trusted personal information (Dall 2004). This suggests that group foragers mimicking their neighbors could be a method of behavioral replication for vigilance strategies. Even if an individual does not mimic a strategy explicitly, the result of repeated mimicry of a tactic (either foraging or being vigilant) through time is an indirectly mimicked strategy.

If we use mimicry of social information as a replicator, the difference in time scales shrinks. The rate at which mutant strategies can invade increases which gives credence to the results from the typically solved dynamical system. Importantly the stable attractors in the system do not change. Thus, the same mechanism as before can partially explain the trend that is observed on short times scales as well. If the group is in an environment which allows it to grow large, lower vigilance strategies will become more common as they are mimicked in the group whereas if the group is in an environment which limits its size, higher vigilance strategies would invade because low vigilance individuals would be more likely to be removed and thus less likely to be mimicked. This last piece of the mechanism requires that the group faces predators frequently relative to innovation which is not always the case. This limits the scope of the social mechanism alone, but the combination of the social and inherited mechanisms can adequately explain the relationship between group size and vigilance both on very long time scales and on shorter ones.

In the short term, ε takes on the meaning of innovation rate, which is the rate at which new behaviors, that will be mimicked, arise. In this case, where innovation rate is comparable to the rate at which group members leave or join, some parameter spaces produce limit cycles as shown in Figures 22 and

23. These limit cycles would be observed as variations of group size and vigilance level throughout a period of time. Using the typical method of numerically solving a dynamical system reveals that innovation rate is associated with the amplitude of variation(Fig. 25). In these parameter spaces, when innovation is high and vigilance changes almost as fast as group size does, there is great variation in group size. When innovation is low there is very little variation in group size. In particular, some parameter spaces produce limit cycles of group size and vigilance where vigilance increases slightly and group size increases in response, then vigilance decreases and group size decreases in turn. when innovation is very uncommon or the magnitude of innovation is very small the amplitude of such a limit cycle may decrease to become close to zero, although it is still a stable limit cycle surrounding an unstable spiral. When large magnitude innovations are common, we may expect that group size experiences very large fluctuations in time. Further support for these conclusions would require further inquiry into the extensions of adaptive dynamics into replication through public information.

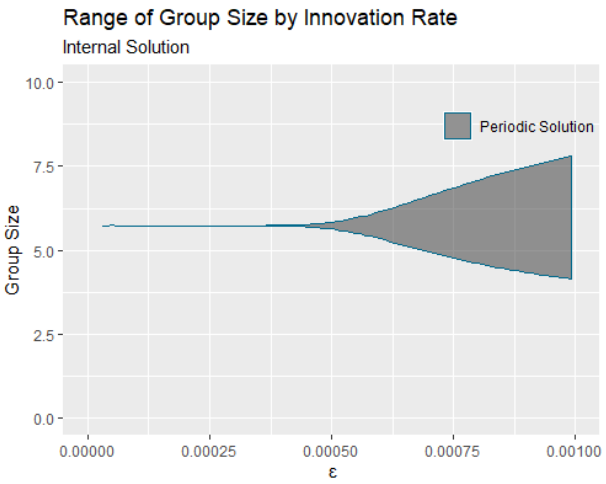

Figure 25 Shows the maximum and minimum group size of the limit cycle found in the typical manner for a range of innovation rates, ε.

Through investigation of both equilibrium solutions with rare low magnitude innovation, as in instinctual behavior, and of solutions where innovation is common, as in inadvertent social information, this model seems to capture the well observed phenomenon of the inverse relationship between vigilance and group size. Doing so with use of pairwise invasion where individuals need not know what strategies the rest of the group is using gets rid of the requirement for behavioral monitoring. When group size is high, low vigilance strategies may invade more easily whereas when group size is limited, most potently by intraspecific competition, low vigilance strategies can not invade and instead higher vigilance strategies resist invasion. Thus I provide an adaptive mechanism by which to support the many eyes hypothesis without relying on behavioral monitoring.

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A Proofs

Proof 1 - Nonuniform convergence of transmission

claim

$$\lim_{N\to\infty} \neg F_N(V) = \begin{cases} 0 & V < 1 \\ 1 & V = 1 \end{cases} \tag{36}$$

proof Recall that

$$\begin{aligned} \neg F_N(V) &= (1 - P_v(1-V))((1-P_N) + P_N \neg F_{N-1}(V))^{N-1} \\ \neg F_1(V) &= (1 - P_v(1-V)) \end{aligned} \tag{37}$$

Consider $\neg F_N(1)$. Clearly $\neg F_1(1) = 1$. Now suppose $\neg F_N(1) = 1$ for some $N \in \mathbb{N}$ and consider $\neg F_{N+1}(1)$.

$$\begin{aligned} \neg F_{N+1}(1) &= (1 - P_v(1-1))((1-P_N) + P_N \neg F_N(1))^N \\ &= (1)((1-P_N) + P_N(1)) = 1 \end{aligned} \tag{38}$$

So by induction$\neg F_N(1) = 1 \quad \forall N \in \mathbb{N}$. Now consider any $V < 1$. Clearly $\neg F_1(V) < 1$. Now suppose $F_N(V) < 1$ for some $N \in \mathbb{N}$ and consider $\neg F_{N+1}(V)$.

$$\begin{aligned} \neg F_{N+1}(V) &= (1 - P_v(1-V))((1-P_N) + P_N \neg F_N(V))^N \\ &< ((1-P_N) + P_N \neg F_N(V))^N \\ &< (1 - P_N(1 - \neg F_N(V)))^N < 1 \end{aligned} \tag{39}$$

so by induction $\neg F_N(V) < 1 \quad \forall V < 1, \forall N \in \mathbb{N}$. Knowing that $\neg F_N(V) < 1$ gives us $\varepsilon > 0$ such that $\neg F_N(V) < 1 - \varepsilon$. To complete the proof we simply note that $\neg F_N(V) < ((1-P_N) + P_N \neg F_{N-1}(V))^{N-1}$ so

$$\begin{aligned} \lim_{N\to\infty} \neg F_N(V) &\leq \lim_{N\to\infty} ((1-P_N) + P_N \neg F_{N-1}(V))^{N-1} \\ &\leq \lim_{N\to\infty} ((1-P_N) + P_N(1-\varepsilon))^{N-1} \\ &\leq \lim_{N\to\infty} (1 - P_N\varepsilon)^{N-1} = 0 \end{aligned} \tag{40}$$

And, because $\neg F_N(V) \geq 0$, squeeze theorem competes the proof. We note that, because $\neg F_N(V)$ is continuous for all $N \in \mathbb{N}$ but $\lim_{N\to\infty} \neg F_N(V)$ is discontinuous, the convergence is necessarily nonuniform.■

Proof 2 - Expression of Change in Internally Controlled Group Size

claim

$$\frac{dN}{dt} = \left(1 + 2N\left(-\log\left(\xi(N)\right) + (1-N)\frac{\xi'(N)}{\xi(N)}\right)\right) \tag{41}$$

proof Recall that group size will grow if and only if the average group member can increase their fitness by allowing another individual into the group. Thus $\frac{dN}{dt} \propto \frac{\partial}{\partial N} w(V,N)$. Fitness is described by

$$\begin{aligned} w(V,N) &= \frac{s_0 V\sqrt{N}}{(1+aV)^{N-1}(1+s_2V)(1-(1-V)P_v)\left(1-\frac{(1-V)NP_v}{C+N}\right)^{N-1}} \\ &= k_0\left(\frac{\sqrt{N}}{\left((1-aV)\left(1-\frac{(1-V)NP_v}{C+N}\right)\right)^{N-1}}\right) \end{aligned} \tag{42}$$

Where k_0 is clearly nonzero under biologically reasonable conditions. Define a function $\xi(N) := (1-aV)\left(1-\frac{(1-V)NP_v}{C+N}\right)$ so we express fitness as

$$w(V,N) = k_0\sqrt{N}(\xi(N))^{1-N} \tag{43}$$

Now take the derivative with respect to N of both sides.

$$\frac{\partial}{\partial N} w(V,N) = k_0\frac{1}{2\sqrt{N}}(\xi(N))^{1-N} + k_0\sqrt{N}\left(\frac{d}{dN}(\xi(N))^{1-N}\right) \tag{44}$$

To compute the derivative, we first must look at the derivative of $\xi(N)^{1-N}$. first we define $y := \xi(N)^{1-N}$ then we take the log then the N derivative of both sides.

$$\begin{aligned} \log(y) &= \log\left(\xi(N)^{1-N}\right) \\ \frac{d}{dN}(\log(y)) &= \frac{d}{dN}((1-N)\log(\xi(N))) \\ \frac{1}{y}\frac{dy}{dN} &= -\log(\xi(N)) + (1-N)\frac{\xi'(N)}{\xi(N)} \\ \frac{dy}{dN} &= \left(-\log(\xi(N)) + (1-N)\frac{\xi'(N)}{\xi(N)}\right)\xi(N)^{1-N} \end{aligned} \tag{45}$$

Substituting this expression back in we arrive at

$$\begin{aligned} \frac{\partial}{\partial N} w(V,N) &= k_0\frac{1}{2\sqrt{N}}(\xi(N))^{1-N} + k_0\sqrt{N}\left(-\log(\xi(N)) + (1-N)\frac{\xi'(N)}{\xi(N)}\right)\xi(N)^{1-N} \\ &= k_0\xi(N)^{1-N}\left(\frac{1}{2\sqrt{N}} + \sqrt{N}\left(-\log(\xi(N)) + (1-N)\frac{\xi'(N)}{\xi(N)}\right)\right) \end{aligned} \tag{46}$$

$k_0\xi(N)^{1-N} > 0$ under reasonable conditions thus it impacts only the magnitude of $\frac{dN}{dt}$ Because the two components change at different time scales we are not concerned with the magnitude, only the sign which is strictly described by the second term. Thus after we find a common denominator, we conclude a reasonable formulation for $\frac{dN}{dt}$ under internal control is

$$\frac{dN}{dt} = \left(1 + 2N\left(-\log(\xi(N)) + (1-N)\frac{\xi'(N)}{\xi(N)}\right)\right) \tag{47}$$

Proof 3 - No Solutions Escape to Infinity

claim Group size is bounded above.
proof We consider $\mathcal{P}(V)$ (Eq. 24) which can be expressed as

$$\mathcal{P}(V) = -Cf(V) + Ng(V) \tag{48}$$

Both f and g are continuous on $[0, 1]$ because they are polynomials, thus, they attain their extrema on that Interval. Also notice that $g(V) > 0$ on that interval. Let $m = \inf g(V), M = \sup f(V)$ so $\mathcal{P}(V) \geq -CM + Nm$. Thus if N is large enough, $\mathcal{P}(V)$ is positive for all V and V will increase to 1. When $V = 1$, both formulations of $\frac{dN}{dt}$ are negative at extremely large N so group size must decrease and so no solution can escape to infinity.■

Proof 4 - Internal Fixed Points Between External Fixed Points

claim When there are two fixed points in the external system, N_I^* is always between them
proof Let$V \in [0, 1]$ such that $\frac{dN_E}{dt}$ has two fixed points. Those fixed points are

$$\{N \in \mathbb{R} | w(V, N) = w(V, 1)\} \tag{49}$$

Let $c = w(V, 1)$ so $\exists N_1, N_2 \in \mathbb{R}$ such that $w(V, N_1) = c = w(V, N_2)$. So by Role's theorem $\exists N^* \in (N_1, N_2)$ such that $\frac{\partial}{\partial N} w(V, N^*) = 0$. This is exactly the condition for the fixed point of the internal system, thus $N_1 < N_I^* = N^* < N_2$. Therefore, because V was arbitrary, whenever the external system has two fixed points, the internal system has a fixed point between them. Because when there are two fixed points one is stable and one is unstable we can say that the manifold of fixed points in the internal system is always between the stable and unstable manifolds in the external system when they exist.■

B Table of Variables and symbols

Symbol	Meaning	Relationship to other variables	(Pg)
	Model Background (2)		
w	Fitness	$w = \frac{\alpha}{\mu}$	2
α	Benefit gained in some time step	$\alpha = \frac{s_0}{(1+aV)^{N-1}} \frac{V}{s_2+V}$	2
μ	Risk of death in some time step	$\mu = (1-(1-V)P_v)\left(1-(1-V)\frac{N}{C+N}P_V\right)^{N-1} \frac{P_0}{\sqrt{N}}$	2
V	Proportion of time spent foraging		2
E	Proportion of time spent being vigilant	$E = 1 - V$	2
s_1	General foraging rate	$\frac{s_0}{(1+aV)^{N-1}}$	2
s_0	Foraging rate for a single individual		2
s_2	Constant proportional to search time		2
a	Intensity of competition		2
	Approximating Transmission (3-7)		
F	Fleeing event		3
$\mathcal{V}$	Seeing a predator event		3
C	Perceiving that there is a predator from a group member		3
P_v	Probability of seeing a predator while being vigilant		3
P_N	Probability of antipredator information Transmission		3
$\neg F_N(V)$	Probability of not fleeing in a group of N individuals	$\neg F_N(V) = (1-P_v(1-V))((1-P_N)+P_N \neg F_{N-1}(V))^{N-1}$	4
C	Inverse of reliability of information	$C = \frac{2(1-P_N)}{P_N}$	5
$P_A(N)$	Probability an individual is attacked in a group of size N	$P_A(N) = \frac{P_0}{\sqrt{N}}$	5
P_0	Probability a single individual is attacked		7
	Pairwise Invasion (7-9)		
w_r	Fitness of a resident with one mutant invader		7
w_m	Fitness of a mutant invader in a resident group		7
$\Delta\tilde{w}$	Fitness differential	$w_r - w_m$	7
K_0	Constants in fitness differential		7
Δw	Adjusted fitness differential for ease of computation	$\frac{\Delta\tilde{w}}{K_0}$	7

Symbol	Meaning	Relationship to other variables	(Pg)
$\mathcal{I}_1$	First isocline on the Pairwise Invasion Plot	$\mathcal{I}_1 = \{(V,u) \in [0,1] \times [0,1] \vert u = V\}$	8
$\mathcal{S}$	Fitness differential Surface	$\mathcal{S} = \frac{\Delta w(u,V)}{V-u}$	7
$\mathcal{I}_2$	Second isocline on the Pairwise Invasion Plot	$\mathcal{I}_2 = \{(V,u) \in [0,1] \times [0,1] \vert \mathcal{S}(u,V) = 0\}$	9
$\mathcal{P}(V)$	Potential change in group fitness from invasion	$\mathcal{P}(V) = \mathcal{S}(V,V)$	9
$\mathcal{P}_4(V)$	Explicit polynomial expression of $\mathcal{P}(V)$	$\mathcal{P}_4(V) = \mathcal{P}(V)$	9
ε	Mutation Rate		9
Group size (10)			
N_E^*	External Ideal Group Size	$N_E^* \approxeq \{N \in \mathbb{R} \vert w(V,N) - w(V,1) = 0\}$	10
N_I^*	Internal Ideal Group Size	$N_E^* = \arg\max_{N \in \mathbb{Z}} w(V,N)$	10